



Exogenous application of gamma-aminobutyric acid (GABA) alleviates the effect of water deficit stress in black cumin (*Nigella sativa* L.)

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ABSTRACT

Water deficit is an abiotic stress factor that negatively affects black cumin (*Nigella sativa* L.) production. Gamma aminobutyric acid (GABA), an endogenous signaling molecule and metabolite, has high physiological and molecular activity in plant cells, which can promote tolerance to water deficit stress, but little information is available on the effect of exogenous application on growth of black cumin. A field experiment over two years was carried out at a farm located in Naqadeh-Urmia, West Azerbaijan, Iran to evaluate the effects of GABA on some agronomic and biochemical attributes of black cumin under water deficit stress conditions. Three irrigation treatments (irrigation after 50, 100, and 150 mm evaporation based on evaporation from class A pan) and four levels of GABA application (0, 0.5, 1.0, and 2.0 mg L⁻¹) were tested. Irrespective of GABA application, the severe water deficit treatment (i.e., irrigation after 150 mm evaporation) provided the lowest seed number per follicle, 1000-seed weight, and seed yield. Increasing water deficit, significantly reduced chlorophyll *a* by 8.2 to 15.8% and chlorophyll *b* by 18.4 to 41.5%, whereas GABA application significantly improved these traits. The application of 2.0 mg L⁻¹ GABA increased chlorophyll *a* content by 6.2% and chlorophyll *b* content by 19.2% compared with control. In addition, GABA application showed a positive and significant effect on soluble sugars content, proline accumulation, and catalase (CAT) activity. The maximum values of these variables were obtained with the application of GABA at 2.0 mg L⁻¹. CAT, peroxidase (POX), and superoxide dismutase (SOD) activity increased with decreasing chlorophyll *a* and chlorophyll *b* contents, whereas soluble sugars and proline content increased with increasing activity of those antioxidant enzymes. Overall, in addition to cellular mechanisms, such as osmoregulation and antioxidant defense, GABA application can improve growth and productivity of black cumin under water deficit stress conditions.

1. Introduction

Black cumin (*Nigella sativa* L.) or simply nigella is an annual medicinal plant of the family Ranunculaceae (D'Antuono et al., 2002). This plant is native to south and southwest Asia and is cultivated in arid and semi-arid regions of Iran (Mozaffari et al., 2000; Ghamarnia et al., 2010). The seeds contain 0.5 to 1.6% essential oil (Ramadan, 2007) and also are rich in a wide range of compounds, such as fixed (non-volatile) oil, mucilage, alkaloids, essential amino acids, tannins, resins, crude fiber, saponins, minerals, and vitamins (Al-Jassir, 1992; Takruri and Dameh, 1998; Ashraf et al., 2006; Ramadan, 2007). Due to several beneficial properties and health effects (e.g., antibacterial, antidiabetic, anti-inflammatory, and others) (Khan, 1999; Burits and Bucar, 2000;

Ali and Blunden, 2003; Singh et al., 2005; Ait Mbarek et al., 2007; Majdalawieh et al., 2010; Jrah Harzallah et al., 2011), black cumin has been used in traditional medicine in Iran for years (Nickavar et al., 2003) and emerges as a miracle herb with a rich historical and religious background due to a wide spectrum of pharmacological potential (Ahmad et al., 2013).

Effective utilization of *N. sativa* for therapeutic purposes as well as for trade will vastly depend upon yield and essential oil production and quality (Datta et al., 2012). However, research on cultivation practices of black cumin is rather limited. Although black cumin is considered a drought tolerant species cultivated in semi-arid regions of the world, water deficit stress still threatens growth and productivity of this plant (Bannayan et al., 2008; Al-Kayssi et al., 2011). Previous research

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showed that black cumin could tolerate water deficit, except when irrigation was terminated at seed formation (Bannayan et al., 2008). In the same study, the minimum seed yield was obtained when irrigation was stopped at the blooming stage, with the number of seeds per plant being the main yield component affected. Drought stress, which is a common phenomenon in arid and semi-arid regions, is a major abiotic factor that can dramatically impact black cumin seedling establishment, plant growth, and seed yield (Ahmadpour Dehkordi and Balouchi, 2012; Haj Seyed Hadi et al., 2016). Hence, water deficit stress can be a serious limiting factor determining black cumin yield.

Generally, water deficit stress occurs when there is a low water potential in plant tissues as a result of low water potential in the soil, high evaporative demand, and a substantial resistance to water flow through the plant (Gao et al., 2002; Tanguilig et al., 1987). The detrimental effects of water deficit stress on growth and seed production of black cumin are mainly due to reduced water flow through the plant, which disturbs cellular metabolic pathways (Ghamarnia et al., 2010; Goswami, 2011; Haj Seyed Hadi et al., 2016). Plant organisms have enzymatic and non-enzymatic mechanisms that compose a fundamental detoxification apparatus for overcoming oxidative damage induced by abiotic stress (Ashraf et al., 2002; Hasanuzzaman et al., 2010). Several antioxidant enzymes, including superoxide dismutase (SOD), catalase (CAT), and peroxidase (POX), maintain the balance between generating and quenching of reactive oxygen species (ROS) in the plant cells within the ascorbate-glutathione (AsA-GSH) cycle that regulates the redox reaction of AsA and GSH (Mittler, 2002; Li et al., 2010; Lotfi et al., 2015).

According to the abovementioned information, the use of compounds that can improve tolerance to water deficit stress through cellular signaling can be beneficial under drought stress conditions. In this regard, GABA (γ -aminobutyric acid), an endogenous signaling molecule involved in plant regulation (Li et al., 2016a), can play an important role in improving growth and productivity of crops under stressful conditions (Kinnersley and Turano, 2000; Hu et al., 2016; Soleimani Aghdam et al., 2016). GABA improved tolerance of winter wheat to high temperature by regulating the endogenous hormone system, protecting membrane stability, increasing the activity of antioxidant enzymes, removing active oxygen species, modulating the balance of C/N metabolism, and lessening yield losses brought by high temperature (Wang et al., 2009). Moreover, GABA application could increase heat tolerance in bentgrass (*Agrostis stolonifera* L.) through accumulating sugars, organic acids, and adjusting osmotic pressure (Li et al., 2016b). Improved drought tolerance with exogenous application of GABA has been reported also in perennial ryegrass (*Lolium perenne* L.) (Krishnan et al., 2013). However, the effects of GABA application on nigella growth and productivity and its involvement in metabolic events of this crop have not been studied. Therefore, the objective of the current study was to examine the effects of GABA application on physiological parameters of growth and yield as well as on essential oil content and antioxidant enzyme activity of black cumin under water deficit stress conditions. Furthermore, the relationships between antioxidant enzymes activity, proline accumulation, soluble sugars, and chlorophyll content were investigated. The research question of this study was set as: does exogenous application of gamma-aminobutyric acid (GABA) improve the response of black cumin to water deficit stress and, if so, by which mechanism(s)?

2. Material and methods

2.1. Field experiments

Two field experiments were conducted in 2014 and 2015 at a farm located in Naqadeh-Urmia, West Azerbaijan, Iran (long. 45° 25', lat. 36° 57', altitude 1307 m) at a location with an annual rainfall of 334 mm and a silty clay soil (Table 1). Some meteorological data of the experimental site during the growing seasons are given in Table 2. The

Table 1

Soil physico-chemical characteristics of the experimental site.

Soil analysis	2014	2015
Physical		
Clay (%)	42	47
Silt (%)	41	31
Sand (%)	17	22
Chemical		
OC (%)	1.27	1.14
Available N (mg kg ⁻¹)	0.16	0.12
Olsen-P (mg kg ⁻¹)	14.1	10.66
Available K (mg kg ⁻¹)	482.12	450.82
pH	7.4	7.6
EC (dS m ⁻¹)	0.31	0.38

experiments were established in a randomized complete block design (RCBD) with a split plot arrangement and three replicates. Three irrigation levels (irrigation after 50, 100, and 150 mm evaporation based on evaporation from class A pan) were considered the main plots and four levels of GABA application (0, 0.5, 1.0, and 2.0 mg L⁻¹) were considered the sub-plots.

All plots consisted of eight crop rows 4 m in length with plant spacing on the row 0.3 m. Plots and blocks were separated by a buffer space of 1.5 m and 3 m, respectively. The seeds were sown on March 22 in 2014 and 2015 in furrows 7 cm apart. The seedlings were thinned at the four-leaf stage to reach a final planting density of about 45 plants per m². GABA foliar application was performed twice in each growing season, once at seedling establishment and once three weeks later. Tween® 20 (a polysorbate-type nonionic surfactant) was added to the spray solution to reduce the surface tension and enhance foliage wetting. Control plants were sprayed using distilled water. Fertilizers were applied according to soil analysis as 150 kg ha⁻¹ urea (soil-incorporated before sowing and broadcast applied at stem elongation), 150 kg ha⁻¹ triple superphosphate and 250 kg ha⁻¹ sulfur (soil-incorporated before sowing). Since the soil analysis showed sufficient level of potassium, no potassium fertilizer was applied. Weeds were manually controlled during growing seasons.

At the end of each growing season (August 6 in 2014 and 2015), when the plants started to turn yellow, but before the opening of the follicles (138 days after sowing), ten plants from each plot were randomly harvested and examined for plant height, follicle number per plant, seed number per follicle, and 1000-seed weight. To determine seed yield and biomass yield, all plants per plot were harvested after ignoring border plants. Harvesting was performed when seed moisture content was 15%. To determine other traits, three separate samples were taken from each plot and an average was calculated from the raw data.

2.2. Extraction of essential oil

Black cumin seeds were shade-dried at room temperature and crushed using a grinder to extract the essential oil. The essential oil (v/w) was isolated from 10 g of the seeds with 100 mL distilled water with conventional hydro-distillation for 4 h, using a Clevenger-type apparatus (Ashraf et al., 2006).

2.3. Soluble sugars content

Tissue of fresh leaves was homogenized with 10 mL distilled water to determine the soluble sugars content. The extracts were stirred and left at room temperature for 1 h. Then, the extracts were centrifuged at 4500 rpm for 20 min. The soluble sugars content was determined according to Bai and Tang (1993) and measured using a glucose standard (expressed as mg g⁻¹).

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